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CLASSIFICATION OF THE AMIOID AND LEPISOSTEOID FISHES.

O. P. HAY.

THE science of ichthyology has within recent years been greatly enriched by the publication of the volumes of Mr. A. S. Woodward's *Catalogue of the Fossil Fishes in the British Museum.* This work is destined not only to give a great impetus to the study of fossil fishes, but also to have an important influence on the higher classification of the living forms. Many changes, based in part on the distinguished author's own researches, in part on the investigations of others, have been made in the ichthyological system, so that we now get new and clearer views of many groups. The author's conclusions, too, are so modestly set forth that others cannot afford to be dogmatic when they differ from him.

A large portion of the third volume of Mr. Woodward's work is devoted to the elucidation of those fishes which have for some time been regarded as forming the groups called "Amioidei" and "Lepidosteoidei." These groups are rejected by Mr. Woodward and the genera are redistributed. Catopterus and its ally Dictyopyge are made a family of the Chondrostei, while Pholidophorus and a number of related genera are removed to the Isospondyli. With this disposition of these forms no one will probably find fault.

The remaining materials are then divided into two suborders, the Protospondyli and the Aetheospondyli. The living representative of the former group is Amia; that of the latter is Lepisosteus. Mr. Woodward says (3, p. xxii): "It is equally impossible to justify the conceptions of the groups 'Lepidosteoidei' and 'Amioidei,' most of the extinct fishes which are commonly ascribed to the former being proved in the catalogue to be much more closely related to the latter."

It is the purpose of the present paper to consider the correctness of Mr. Woodward's disposition of the fishes here referred to.

The basis for the establishment of the two new suborders is found in the condition of the vertebral axis. In both groups the notochord may or may not be persistent. In the Protospondyli, if the notochord is "more or less replaced by vertebræ, the pleurocentra and hypocentra in part of the caudal region remain distinct even when fully developed." In the Aetheospondyli, on the other hand, we find the "pleurocentra and hypocentra usually fused, never forming alternating disks or rings." In fact, in all the genera admitted to the latter suborder this fusion of vertebral elements has occurred, while all genera devoid of what are regarded as pleurocentra and hypocentra, or, possessing them, do not have them fused, are relegated to the Protospondyli. That is, there are no Aetheospondyli with distinct pleurocentra and hypocentra. Furthermore, two genera which technically belong to the Aetheospondyli are referred justly, no doubt, to the Protospondyli. These are Histionotus and Neorhombolepis. We have no evidence whatever presented that they possess, even in the tail, distinct and alternating pleurocentra and hypocentra.

A word may be permitted at this point regarding relation of the pleurocentra and hypocentra to the notochordal sheath. Mr. Woodward constantly speaks of these elements as being developed in the sheath of the notochord.[1] This, so far as the Teleostomi are concerned, is an error, as has been demonstrated by the observations of many investigators. In the elasmobranchs the vertebral centra are formed principally from cartilage which has invaded the inner sheath of the notochord, and this cartilage may undergo extensive calcification. The same appears to be true of the vertebral axis of the Dipnoi. In the Teleostomi no cartilage develops within the notochordal sheath; neither do the ossifications of the vertebral centra originate there. If the sheath ever becomes ossified it is a secondary process.

It is evident that Mr. Woodward regards as a pleurocentrum any ossification in or in contact with the dorsal portion of the notochordal sheath. He would probably further limit the definition to ossifications arising distinct from the bases of the neural arches. Any similar ossification on the ventral side of the notochord would, I suppose, be regarded as a hypocentrum. At least, no other elements are mentioned as occurring and taking part in the formation of the vertebræ. It is nevertheless true that other elements do exist, and in many fishes enter into the construction of the definitive vertebral centra. These elements, known in their primitive condition as intercalated cartilages, are present in Acipenser and in Polyodon and remain permanently distinct.

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[1] See pp. 80, 132, 164, 190, 195, 287, 374.

In my investigations on the vertebral column of Amia,[1] I showed that these intercalated elements are of the greatest importance in the formation of the adult vertebral centra. I discovered that in the tail region there are, for each muscular segment, eight cartilages, *viz.*, the bases of the two halves of the upper arch, the bases of the two halves of the lower arch, a right and a left upper intercalated cartilage, and a right and a left lower intercalated cartilage (Fig. 1). At a certain stage ossification starts on the surface of each of these cartilages.

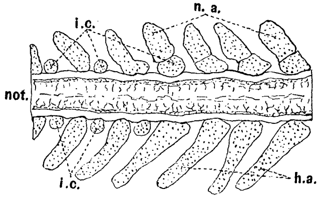

FIG. 1.

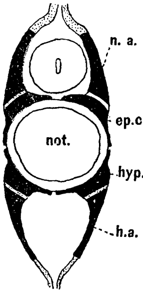

FIG. 2.

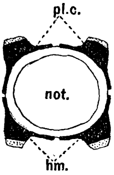

FIG. 3.

FIG. 1. — Longitudinal section of vertebral axis of young Amia, taken a little to one side of the mid-line. *i.c.*, intercalated cartilage; *n.a.*, neural arches; *h.a.*, hæmal arches; *not.*, notochord. At the right hand of the figure the upper intercalated cartilages have pushed themselves under and support the neural arches. In this region, also, the lower intercalated cartilages are wanting. The figure is from a section in the tail where vertebræ of the ordinary form change to those consisting of two distinct rings.

FIG. 2. — A diagrammatic section across one of the arch-bearing vertebral rings of the tail of young Amia. The dotted areas represent cartilage; the black represent the layer of bone covering the underlying cartilage. *ep.cm.*, the epicentral ossifications; *hyp.c.*, the hypocentral ossifications; *n.a.*, neural arch; *h.a.*, hæmal arch; *not.*, notochord.

FIG. 3. — A diagrammatic section through one of the archless vertebral rings of young Amia. *pl.c.*, pleurocentral ossifications; *hm.*, hæmacentral ossifications. Union of the four ossifications will produce a complete ring.

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[1] Publications of Field Columbian Museum, *Zool. Ser.*, vol. i, No. 1.

Those ossifications starting from the bases of the arches, upper and lower of each segment, extend themselves (Fig. 2) and finally unite and form a ring of bone around the notochord, and lying outside of its sheath. This ring is the so-called "hypocentrum," supposed hitherto to arise from the upward growth of elements situated on the lower side of the notochord. The ossifications connected with the four intercalated cartilages (Fig. 3) spread until they meet, and thus produce another ring of bone around the notochord, the so-called "pleurocentrum," hitherto held to be the product wholly of elements situated on the upper side of the notochord. It thus becomes evident that each of the two rings of the muscular segment has another pair of elements entering into its composition besides the pair usually attributed to it. It may further be seen that the element which develops from the bases of the upper arch, the epicentrum, may easily be mistaken for the true pleurocentrum, which in reality has its origin in the upper intercalated cartilages.

In the abdominal region of Amia I found that the lower intercalated cartilage is apparently wanting. On the other hand, the upper ones, which give rise to the pleurocentra, become greatly expanded, push themselves under the bases of the upper arches immediately behind, and suppress the ossifications that might be expected to arise there (Fig. 4). The pleurocentra thus come to support the upper arches, and, growing downward, coalesce with the up-growing hypocentra to form the completed vertebral centrum. It will be seen that in Amia there are three kinds of vertebral rings, *viz.*, those formed from the union of the bases of the upper arches with the bases of the lower arches, those from the intercalated cartilages, and those partly from bases of lower arches and partly from the upper intercalated cartilages.

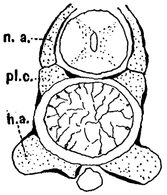

FIG. 4. — Section through an abdominal vertebra of young Amia, 23 mm. long. *h.a.*, base of hæmal arch = hypocentrum; *pl.c.*, pleurocentrum bearing the neural arch, *n.a.*

Now, how does ossification take place in the vertebral column of Lepisosteus, the living representative of the Aetheospondyli? Certain stages have not yet, so far as I am aware, been worked out, but enough seems to be known to enable us to reach fairly good conclusions. It appears that in an early stage the notochord with its sheath becomes surrounded by a tube of cartilage.[1] The bases of the upper and the lower arches are continuous with this tube (Fig. 5, *h.a.*). Midway between the bases of the successive arches the tube becomes thickened into a ring (Fig. 5, *i.c.*), while on each side, just between the base of each upper arch and that of the corresponding lower arch, there is a gap in the cartilaginous tube. Now, it appears to me quite certain that the thickened ring of cartilage is composed of the four coalesced intercalated cartilages; and Dr. Gadow and Miss Abbott entertain the same view.[2] The tube is produced by the coalescence of these with one another and with the bases of the arches. When ossification sets in, the bony centers spread over the cartilage, probably from the bases of the arches, and, forming a ring, bind the arcualia of each segment together. No separate ossifications develop in the rings of intercalated cartilages, but these become divided each into an anterior and a posterior half, the anterior half forming the posterior end of the vertebra in front, the posterior half the anterior end of the vertebra behind. In Lepisosteus, therefore, the vertebral elements derived from the bases of the arches gain complete ascendency over the intercalated elements; in Amia, at least, the upper intercalated elements remain distinct and take a prominent part in the formation of the centrum.

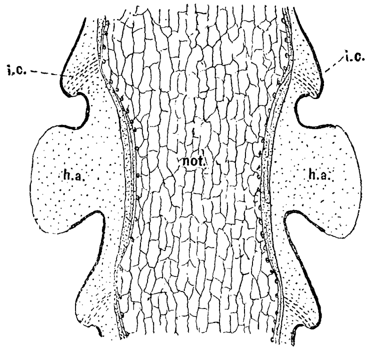

FIG. 5. — Horizontal section through notochord of young Lepisosteus. After Balfour. Cartilage is dotted; the bone shown by heavy black lines. *h.a.*, the bases of the hæmal arch: *i.c.*, the ring of coalesced intercalated cartilages. They are represented as undergoing transverse division.

There is nothing to indicate that the vertebral rings of any of the genera assigned by Mr. Woodward to the Aetheospondyli have had a mode of development essentially different from that of our Lepisosteus. Their vertebral centra have probably been produced by the fusion of the ossifications arising in the upper arches with those of the lower arches. We do not need to disturb these genera.

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[1] Balfour and Parker, *Development of Lepidosteus*, Mem. Ed., vol. i, p. 785, pls. xli, xlii.

[2] *Phil. Trans. Roy. Soc.*, vol. clxxxvi, p. 214, 1895.

Among the Protospondyli we find the nearest allies of the Amiidæ in the family Eugnathidæ. Here we discover abundant evidences of the presence of true pleurocentra. They are shown to be such by the varying positions of the neural arches on them. Neural arch and epicentrum, being ossified portions of the same arcuale, to use Gadow's convenient term, remain in direct contact, even when not coössified. When the epicentrum is not developed, the pleurocentrum may wholly or only partially push itself under the arch. Whenever we find two distinct rings for each segment, the upper and the lower arches are connected with the same ring, as shown in Fig. 6, which represents the vertebræ in the tail of Eurycormus. In the abdominal region of Eurycormus the arch-bearing ring is apparently complete and carries the arches, while the pleurocentra are wedged in between them (Fig. 7); but the hæmacentra, which make up the lower half of the archless rings in Fig. 6 (*hm.*), are wanting. A little further reduction of the epicentra leads to the condition found in Callopterus (Fig. 8) and some of the species of Caturus. We may be sure that species of Caturus which have not yet revealed ossified vertebral elements nevertheless possessed these elements in some form, though possibly only

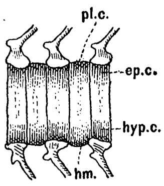

FIG. 6.

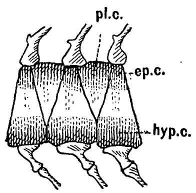

FIG. 7.

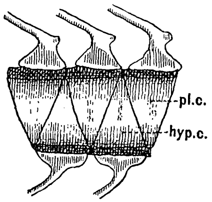

FIG. 8.

FIG. 6. — From tail of Eurycormus. After Zittel. Shows the arch-bearing rings formed by union of epicentra, *ep.c.*, and hypocentra, *hyp.c.*; also the archless rings formed by union of pleurocentra, *pl.c.*, and hæmacentra, *hm.*

FIG. 7. — From abdominal region of Eurycormus. After Zittel. Hæmacentra wanting.

FIG. 8. — From abdominal region of Callopterus. After Zittel. Both hæmacentra and epicentra are aborted, leaving only the pleurocentra, *pl.c.*, and the hypocentra, *hyp.c.* This represents one stage in the abdominal region of Amia.

feebly ossified. Among the Macrosemiidæ, as we are informed, Ophiopsis possessed "completed annular pleurocentra and hypocentra, alternating in the caudal region." These are doubtless true pleurocentra. Mr. Woodward has presented a figure of a portion of the vertebral column of Notagogus.[1] This closely resembles that of the young Amia, as shown by my own figures (Figs. 1–4). Histionotus is not represented as possessing distinct pleurocentra and hypocentra; but the figure in Dr. Zittel's *Handbuch* (vol. iii, Fig. 231) shows each of the vertebral rings as having an oblique position, as though alternating component elements had united. Compare this figure with that of Callopterus, *Handbuch*, p. 231, Fig. 243.

In the Pachycormidæ the vertebral elements are feebly developed; at most, feebly ossified. Nevertheless, they are present in Euthynotus. If we may rely on Dr. Zittel's figure of the vertebral column of this genus, the arch-bearing rings were nearly complete; but there were small pleurocentra wedged in between them.

Taking all things together, we cannot doubt that the vertebral axis of the Amiidæ, the Eugnathidæ, the Macrosemiidæ, and the Pachycormidæ conforms to the same plan of development, and that this is quite different from that of the Lepisosteoid series.

When we come to examine the vertebral structures of the Semionotidæ and of the Pycnodontidæ, we find a very different condition. In many genera, indeed, the vertebral elements are as feebly developed as in some of the Eugnathidæ. In Lepidotus, however, vertebral rings are present; but there are no evidences of the presence of two rings for each muscle segment in any part of the vertebral column. Mr. Woodward states that the rings of Lepidotus seem to consist each of four sectors, each of which bears an arcuale. That is, they are just such rings as those which bear the arches in the tail of Amia (Fig. 2) and such as occur in Lepisosteus. We find no proofs in any member of the family that the intercalated cartilages were ossified, or that they manifested any tendency to assume special importance.

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[1] *Catalogue*, vol. iii, pl. iii, Fig. 10.

I do not see how, in the pycnodonts, the expansions of the neural and hæmal arches can be regarded as essentially different from the epicentra and hypocentra of the tail of the young Amia. They are indeed continuous with the corresponding arches; but so, too, are the vertebral centra of many other fishes. We do not know that the ossifications of the arches of Lepisosteus are at any time distinct from the central ring. That the superior expansions lying upon the notochord of the pycnodonts are continuous with the upper arches is evidence that these expansions do not originate from pleurocentra. The intercalated elements appear to have been suppressed or nearly so, since the bases of the arches in some genera are suturally connected, thus contributing to the rigidity of body of these remarkable fishes.

I conclude, therefore, that we have here two distinct series of fishes to deal with. In the one series the intercalated elements are never of special importance and do not form distinct ossifications. The vertebral centra, when developed, arise principally or altogether from coalescence of the bases of the upper and the lower arches. This series will include the Semionotidæ, the Pycnodontidæ, the Lepisosteidæ, and the Aspidorhynchidæ. The other series will contain those fishes in which there is an evident tendency for the pleurocentrum to usurp the place and function of the ossifications that should arise in the bases of the upper arches. This series will embrace the Macrosemiidæ, the Eugnathidæ, the Amiidæ, and the Pachycormidæ. That is, I believe that Mr. Woodward has gone too far in his transference of genera from the Lepisosteoid to the Amioid series.

As regards the systematic value and kinship of the two groups, it seems to me that they rank no higher than suborders of a distinct order of Actinopterygia. The two suborders are more closely related to each other than to the Chondrostei, or even to the Isospondyli, although the latter order has probably taken its origin from the Amia-like fishes.

I believe that the characters on which my groups of these fishes have been founded indicate two very distinct lines of development, and lines of such a nature that when once entered on there could have been no passage across from the one to the other. Mr. Woodward's groups appear to be based on characters which are rather degrees in the development of the vertebral rings; and, indeed, Amia, a protospondylous fish, would, according to the definitions given, belong to the Aetheospondyli had the fusion of "pleurocentra" and "hypocentra" been carried out a little further in the tail.

In both of the groups proposed there are genera in which, so far as we now know them, the tendencies of the vertebral elements had as yet hardly made themselves manifest. The Lepisosteoid series has, in its vertebral structures, remained closer to the primitive condition; and its members are, therefore, rather more "protospondylous" than those of the other group.

It may be permitted me in conclusion to correct an unfortunate error that I made in a paper contributed to the *American Naturalist*, vol. xxxi, p. 402, 1897. I there stated that the arches, neural and hæmal, originate at a later period in the development of the young fish than do the intercalated cartilages. They are developed earlier, and the error was due to a slip of the pen.

U. S. Nat. Museum,
March 22, 1898.